



Adaptive responses of nitric oxide (NO) and its intricate dialogue with phytohormones during salinity stress

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ABSTRACT

Nitric oxide (NO) is a gaseous free radical that acts as a messenger for various plant phenomena corresponding to photomorphogenesis, fertilisation, flowering, germination, growth, and productivity. Recent developments have suggested the critical role of NO in inducing adaptive responses in plants during salinity. NO minimises salinity-induced photosynthetic damage and improves plant-water relation, nutrient uptake, stomatal conductance, electron transport, and ROS and antioxidant metabolism. NO contributes active participation in ABA-mediated stomatal regulation. Similar crosstalk of NO with other phytohormones such as auxins (IAAs), gibberellins (GAs), cytokinins (CKs), ethylene (ET), salicylic acid (SA), strigolactones (SLs), and brassinosteroids (BRs) were also observed. Additionally, we discuss NO interaction with other gaseous signalling molecules such as reactive oxygen species (ROS) and reactive sulphur species (RSS). Conclusively, the present review traces critical events in NO-induced morpho-physiological adjustments under salt stress and discusses how such modulations upgrade plant resilience.

1. Introduction

Soil salinity poses a severe threat to global food security since most food crops are glycophytes and cannot grow well under a saline regime. The excessive presence of salt in soil with an electrical conductivity of ≥ 4 dSm⁻¹ characterises saline land (USSS, 2005). Over 800 million hectares are salt-affected, accounting for about \$27 billion in global economic loss annually (Qadir et al., 2014). Multiple anthropogenic activities including industrialisation and agricultural malpractices, accelerate soil salinisation. The high salt concentrations in the soil make the uptake of water and nutrients difficult for the plant. While plant-water imbalance stages osmotic stress, selective uptake and accumulation of salt ions e.g., Na⁺, Cl⁻, in inter- and intracellular spaces confer ionic stress (Munns, 2005). Salinity-induced osmotic and ionic stress upregulates the production of reactive oxygen species (ROS) (van Zelm et al., 2020). ROS act as signalling molecules for different

metabolic pathways. However, its overaccumulation confers cellular damage by oxidising lipids, proteins, and genetic materials (Baxter et al., 2014; Halliwell and Gutteridge, 2015). These highly unstable oxygen intermediates are typically generated as by-products of vital physiological processes such as photosynthesis and respiration (Foyer, 2018). Given the usual production of ROS, each plant compartment has an inbuilt antioxidative system to keep ROS production in check (Gill and Tuteja, 2010; Mukarram et al., 2021). Nevertheless, accelerated ROS during a stressful environment disturbs ROS-antioxidant homeostasis and confers oxidative stress (Noctor et al., 2018; Mukarram et al., 2022). Thus, ionic, osmotic, and oxidative stress are the chief chariots for salinity-induced growth, development, and productivity constraints in plants (Yang and Guo, 2018). Similar salt-induced restrictions on plant productivity were observed in many crops of economic importance including rice, wheat, barley, and maize (Munns et al., 2006; Widodo Patterson et al., 2009; Zörb et al., 2019; Mukarram et al., 2023).

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The nitric oxide (NO) paradigm has observed a decisive shift from an endogenous toxic free radical in mammals to a potent signalling molecule with many diverse actions in phylogenetically different plants (Lamattina et al., 2003; Yu et al., 2014). Feeding studies established that NO actively participates in signal transduction for many physiological processes, such as photomorphogenesis, fertilisation, flowering, germination, growth, and productivity (Domingos et al., 2015; Kolbert et al., 2019). It upregulates plant-water relation, chlorophyll synthesis, photosynthetic efficiency, and antioxidant machinery in many crops (Procházková et al., 2013; Del Castello et al., 2019). Furthermore, NO grabs special attention during stressful environments, given its intrinsic dialogue with plant metabolism to confer stress-adaptive responses (Simontacchi et al., 2015; Fancy et al., 2017). NO accumulation is thought to improve plant growth and development under abiotic stress (Corpas et al., 2011; Farnese et al., 2016). These responses are relevant during salinity stress as well. During salinity, NO can target multiple active sites in the chloroplast to improve chloroplast ultrastructure and biosynthesis, photosystem II efficiency, Calvin cycle, stomatal conductance, RuBisCO activity, ion homeostasis, plant water relation, ROS metabolism, and antioxidant activity (Ahmad et al., 2016; Hasanuzzaman et al., 2018; Bhardwaj et al., 2021; Li et al., 2022).

Furthermore, NO promptly reacts with oxidants, antioxidants, phytohormones and other signalling moieties under salinity stress. Multiple reports suggest a complex signal cascade among NO and plant hormones such as auxin (indole-3-acetic acid; IAA), gibberellin (GA), cytokinins (CKs), ethylene (ET), salicylic acid (SA), strigolactones (SL), and brassinosteroids (BRs) for stress mitigation (Freschi, 2013; Simontacchi et al., 2013; Asgher et al., 2017). This intricate signalling cascade contributes to the fine-tuning of physiological processes essential for plant survival and growth under salinity stress. NO has an essential role in ABA-mediated stomatal closure through upregulating mitogen-activated protein kinase (MAPK) and cyclic GMP (cGMP) activity (Neill et al., 2008). NO interaction with SA and ET improves photosynthesis and $\text{Ca}^{2+}/\text{Mg}^{2+}$ uptake while reducing H_2O_2 accumulation and Na^+ uptake (Siddiqui et al., 2011; Hasanuzzaman et al., 2018). Considering the active participation of NO in plant physiology and its crosstalk with various metabolic pathways, we indulge here in a timely discussion on the role of NO and its intricate signalling with phytohormones under salinity stress in this review.

2. NO biosynthesis

Nitric oxide (NO) is a bioactive and diffusible gaseous free radical with multifaceted physiological roles in plants (Röszer, 2014). Being an intra- and intercellular messenger, NO potentially induces several processes in plants, including stomatal closure, chloroplast biogenesis, cell wall synthesis, the expression of defence-related genes, programmed cell death, pollen tube growth, root development and seed germination (Neill et al., 2003; Lamotte et al., 2005; Tun et al., 2006). Endogenous biosynthesis of NO has been reported in green algae (Mallick et al., 1999; Foresi et al., 2010), lichens (Expósito et al., 2022), cyanobacteria (Mallick et al., 1999; Fabisik et al., 2023), and in several higher plant species (Röszer 2012b; Röszer, 2014). It is well-documented that NO synthesises endogenously in plants. Two primary sources of NO production have been proposed in plants i.e., nitrate reductase-dependent NO production enzymatically or non-enzymatically, and via arginine through NOS (nitric oxide synthase) as in mammals. The first enzymatic and best-characterised pathway of NO production is the Nitrate Reductase (NR) pathway. Nitrate reductase is well-known to reduce nitrate into nitrite, utilising NAD(P)H as a co-factor. However, it catalyses one electron transfer from NAD(P)H to nitrite to produce NO. Nitrate reductase occurs in two forms i.e., cytosolic and plasma membrane-bound forms in plants. An *in vitro* experiment on sunflower and sugarcane confirmed the increased release of NO from the plants at night after improving the NO_3 content of the nutrient culture solution (Wildt et al., 1997). Multiple *in vitro* (Yamasaki et al., 1999; Yamasaki

et al., 1999) and *in vivo* (Rasul et al., 2012; Santolini et al., 2017) experiments have confirmed the ability of NR to reduce NO_2 into NO via NADH-dependent process. Subsequently, NO production was associated with other nitrite-dependent pathways in plants. In the early twenties, a new angle was introduced to our knowledge of NR-dependent NO synthesis. Nitrite-dependent NO synthesis can also be achieved by plant mitochondria (Planchet et al., 2005), similar to animal mitochondria (Kozlov et al., 1999). The synthesis of NO was found to be interrupted by the inhibitors that affect mitochondrial electron transport, suggesting that nitrite reduction is driven by the electron of mitochondrial electron transport. This scenario highlights that NO release depends on NR for nitrite production under hypoxic or anoxic conditions, but the source of the bulk NO output from nitrite is mitochondria. However, this reaction would depend on the cytosolic ratio of nitrate to nitrite (Tischner et al., 2004). Moreover, other enzymatic sources of NO production including xanthine oxidase, copper amine oxidase 1, and cytochrome P450, have also been reported in plants. A plasma membrane-bound enzyme, Ni-NOR (310 kDa), has been reported to reduce nitrite into NO utilising cytochrome *c* as an electron donor in tobacco plants (Stöhr et al., 2001). Bethke et al. (2004a) reported a non-enzymatic reduction of nitrite into NO by ascorbic acid at acidic pH in the apoplast of aleurone cell layers of barley. Two hormones (ABA or gibberellin) acidify the apoplastic medium and are found responsible for this reaction. Moreover, other non-enzymatic sources that catalyse the reduction of NO_2 into NO are phenolic compounds such as catechin, carotenoids (Cooney et al., 1994), and polyamines such as spermine and spermidine (Tun et al., 2006). Besides nitrite-dependent NO synthesis, arginine-dependent NO synthesis, analogous to that employed by animal NOS, was also reported in plants (Wendehenne et al., 2001).

There is no proof of an animal NOS-like enzyme in plants. However, two enzymes i.e., a variant isoform of the P protein of the glycine decarboxylase complex in tobacco and AtNOS/AtNOS1 (a member of the circularly permuted GTPase family) in *Arabidopsis thaliana*, were identified (Guo et al., 2003). These two plant enzymes are supposed to have biochemical properties similar to animal cNOS. However, they have no sequence similarity to any known animal NOS (Crawford et al., 2006; Santolini et al., 2017). NOS involves FAD, FMN, BH4, calcium, and calmodulin to catalyses oxygen and NADPH-dependent oxidation of NO and citrulline in a complex reaction (Palavan-Unsal and Arisan, 2009). AtNOS1 was identified during the screening of *Arabidopsis thaliana* genes that encode proteins with identical sequences reported in NO synthesis in the snail *Helix pomatia* (Guo et al., 2003). AtNOS1 belongs to a novel family of putative NOS found only in bacteria and eukaryotes and shows no similarity to plants iNOS (Zemojtel et al., 2004). Currently, AtNOS1 accords the corroboration of arginine-dependent NO synthesis, and it is the only known arginine-dependent NOS in plants. Several other mechanisms and genes are supposed to be involved in NO synthesis because mutations in this gene hamper NO synthesis *in vivo* entirely (Crawford, 2006). The data, as of now, stipulates the possibility that AtNOS1 encodes an NOS enzyme that acts similarly to the constitutive class of mammalian NOS enzyme, exhibiting Ca^{2+} mediated regulation with less transcriptional control. However, the protein's sequence and biochemical analysis indicate how it can conciliate the oxidation of arginine to produce NO by using NADPH (Crawford, 2006).

3. NO-mediated salt stress tolerance in higher plants

Nitric oxide supports several physiological processes needed for plant growth and development and regulates salt-induced responses (Table 1). Its production is significantly upregulated under saline conditions. The available literature on salt stress tolerance through the actions of NO is controversial to some extent, and other factors including plant species types, age, duration, and degree of salt stress treatment, play critical roles in salt stress tolerance (Hasanuzzaman et al., 2018; Jahan et al., 2021). NO is supposed to act like an antioxidant that halts chain reactions initiated under oxidative stress by reactive oxygen

Table 1
Adaptive responses of exogenous NO application in higher plants under saline settings.

| Plant name | Experiment type | Degree of salt stress | NO treatment | Response | References |
|-------------------------------|----------------------------------|-------------------------------|---|---|-----------------------|
| <i>Triticum aestivum</i> | Pot experiment | 150–300 mmol/L NaCl | 0.1 and 1 mmol/L SNP | SNP treatment limited the oxidative stress and enhanced the activities of SOD and CAT under salt stress. | Ruan et al. (2002) |
| <i>Kosteletzkya virginica</i> | Hydroponic culture medium | 0, 100, 200, 300, 400 mM NaCl | 60 μ M SNP. | Salt treatment maximised the Na^+/K^+ ratio, decreased the fresh and dry weights, and enhanced the activities of POD and SOD. However, SNP treatment under salt stress further increased the activities of POD and SOD. | Guo et al. (2005) |
| <i>Zea Mays</i> | Pot Experiment | 100 mmol/L NaCl | 100 μ M SNP | SNP treatment increased dry mass, chlorophyll content, K^+/Na^+ ratio, and Spd + Spm/Put ratio and decreased electrolyte leakage under salt stress. | Zhang et al. (2006) |
| <i>Hordeum vulgare</i> | Pot experiment | 50 mM NaCl | 50 μ M SNP | Treatment of SNP under salt stress decreased ion leakage, carbonyl content, MDA and H_2O_2 contents, and enhanced antioxidant enzyme activities (SOD, APX, and CAT). SNP also enhanced ferritin accumulation in chloroplasts. | Li et al. (2008) |
| <i>Oryza sativa</i> | Pot experiment | 80 mM NaCl | 0.2 mM SNP | Salt stress hampered the photosynthetic activity and reduced growth. Reduction in sub-stomatal CO_2 concentrations and stomatal conductance were also reported. SNP treatment lowered the harmful effects of salt stress by improving photosynthetic activity. | Habib et al. (2016) |
| <i>Glycine max</i> | Pot experiment | 80 mM NaCl | 10 μ M DETA/NO | Salt stress hampered the growth of plants in terms of a decrease in root, shoot, and nodule weights. Moreover, an increase in H_2O_2 and APX activities was also reported. NO treatment reverses the harmful effects of salt stress and, further increases the activity of APX and lowers the level of H_2O_2 . | Egbichi et al. (2014) |
| <i>Brassica juncea</i> | Pot experiment | 100 mM NaCl | 100 μ M NO | Salt stress inhibited growth and photosynthetic activity. Plants treated under salt stress exhibited a distorted chloroplast thylakoid system. NO treatment restored the normal functioning of plants via improving photosynthetic machinery antioxidant enzymes and decreasing ion accumulation. | Fatma et al. (2016) |
| <i>Cicer arietinum</i> | Pot experiment | 50–100 mM NaCl | 50 μ M SNP | Salt stress reduced growth, Chl a, Chl b, and total chlorophyll content and enhanced MDA and H_2O_2 contents. SNP treatment significantly alleviated oxidative stress and improved growth. | Ahmad et al. (2016) |
| <i>Capsicum annum</i> | Pot experiment | 150 mM NaCl | 150 μ M SNP | Salt stress lowered the mineral element uptake, photosynthetic rate, stomatal conductance, intercellular CO_2 concentration, and transpiration rate. NO application significantly reduced the MDA and H_2O_2 contents and improved the above-mentioned parameters. | Shams et al. (2019) |
| <i>Brassica chinensis</i> | Seed germination in Petri dishes | 100 mM NaCl | 5–100 μ M SNP | Salt stress potentially inhibited the seed germination potential, vitality index, germination index, and growth of radicles and plumules. Pre-treatment of SNP improved the contents of proline, soluble sugars, and K^+ and decreased the content of Na^+ in radicles and plumules. | Ren et al. (2020) |
| <i>Crocus sativus</i> | Pot experiment | 50 and 100 mM NaCl | 10 μ M SNP | Salt stress-induced MDA and H_2O_2 contents and decreased growth and photosynthetic pigment contents. No treatment significantly alleviated the oxidative stress and improved the growth of plants. | Babaei et al. (2021) |
| <i>Solanum lycopersicum</i> | Pot experiment | 150 mM NaCl | 10 μ M nitrosoglutathione GSNO (NO donar) | Transcriptome analysis of NO-treated plants identified several genes involved in the alleviation of salt stress. NO application increased the synthesis of IAA (Indole acetic acid) and salicylic acid and decreased ethylene and ABA in salt-stressed plants. | Wei et al. (2022) |

species or directly scavenges free radicals (Tian and Lei, 2006). A study on *Brassica rapa* suggested that NO mitigates the damaging effects of salinity stress via minimising oxidative stress and accelerating the degradation of proline, facilitating the plant to be more adaptable under a stressful environment (Lopez-Carrion et al., 2008). Plants undergo cellular adaptation by maintaining Na^+ concentration in the cytoplasm by controlling Na^+ involvement across the plasma membrane and tonoplast under salt stress (Siddiqui et al., 2011). NO induces K^+ uptake while minimising the uptake of Na^+ , thus maintaining ion homeostasis and providing resistance to plants under salinity stress conditions. NO induces the expression of vacuolar H^+ -ATPase and H^+ -PPase under salt stress, which helps detox cells by triggering Na^+/H^+ ion exchange (Zhang et al., 2006). For instance, NO application uplifted the Na^+/H^+ antiport and tonoplast H^+ -ATPase activity in maize (Zhang et al., 2006). It spiralled Na^+ compartmentalisation and salt tolerance.

3.1. Seed germination

NO exerts a dynamic influence on seed germination under salinity stress, operating as a vital regulator of critical physiological and molecular processes (Goyal et al., 2021). When seeds encounter high salt concentrations in the soil, NO acts as a pivotal mediator that balances

the delicate interplay between dormancy and germination (Zheng et al., 2009; Liu et al., 2019). At lower concentrations, NO mitigates seed dormancy by facilitating the breakdown of abscisic acid (ABA), an inhibitory hormone (Hancock et al., 2011; Kataria et al., 2022). This enables the seeds to transition into germination more efficiently. NO and ET can interact synergistically to regulate seed germination under salinity stress (Arc et al., 2013). NO has been shown to positively influence ET production, possibly by upregulating the expression of genes involved in ET biosynthesis (García et al., 2010). ET, in turn, may enhance the sensitivity of seeds to NO, creating a feedback loop that facilitates the coordination of their actions during germination (Castillo et al., 2018). Moreover, both NO and ET play a crucial role in maintaining the equilibrium of reactive oxygen species (ROS), which are essential signalling molecules but can become detrimental when overly accumulated (Fan et al., 2013; Khator and Shekhawat, 2020). By scavenging excess ROS, NO shields seeds from oxidative damage, ensuring the integrity of cellular components necessary for successful germination (Kopyra and Gwóźdz, 2003; Hasanuzzaman et al., 2021). Additionally, NO's interaction with cell wall-modifying enzymes supports the softening of seed coats, aiding seedling emergence. By modulating ion fluxes, NO helps regulate water and ion balance, preserving turgor pressure and enabling seeds to imbibe water for germination (Fan et al.,

2013; Alnusairi et al., 2021).

3.2. Growth and root development

NO operates as a multifaceted signalling molecule, intricately modulating various aspects of growth to mitigate the adverse effects of high soil salt levels (Bhardwaj et al., 2021). By influencing root and shoot growth, NO assists in maintaining a balanced plant structure under stress conditions (Egbichi et al., 2014; Singh et al., 2016). Furthermore, NO-mediated enhancement of antioxidant defence mechanisms serves as a shield against oxidative damage induced by salt-induced ROS accumulation, thereby safeguarding cellular integrity and promoting sustained growth (Habib et al., 2016). Through interactions with ion channels and transporters, NO helps exclude toxic sodium ions and maintain cellular osmotic balance, fostering optimal growth conditions (Campos et al., 2019). NO's influence extends to root architecture, where it stimulates lateral root formation, allowing plants to explore a larger soil volume for essential resources (Badem and Söylemez, 2022). Moreover, NO-mediated alterations in cell wall properties facilitate root elongation and penetration through saline soils (Jing et al., 2022). By regulating ion transport mechanisms, NO maintains a delicate balance of Na⁺ and K⁺ ions, crucial for preserving cellular integrity and osmotic equilibrium. This action not only prevents excessive sodium accumulation in the roots but also promotes efficient nutrient uptake and promotes growth (Shams et al., 2019; Sardar et al., 2023). The collaborative efforts of NO in promoting lateral root growth, adapting cell walls, and regulating ion dynamics enhance root functionality under salinity stress, enabling plants to better access water and nutrients, thus fortifying their overall resilience (Santos et al., 2020).

3.3. Photosynthesis and stomatal regulation

NO emerges as a pivotal regulator in the intricate interplay of photosynthesis and stomatal regulation under salinity stress in plants. NO's role extends to the modulation of guard cell signalling pathways, which intricately govern stomatal behaviour (Neill et al., 2008; Liao et al., 2023). Through its involvement, NO finely tunes the stomatal aperture, resulting in optimised water use efficiency by reducing transpiration rates, thereby preserving vital water resources under conditions of osmotic stress (Hayat et al., 2013; Bhardwaj et al., 2020). Concurrently, NO's interaction with the photosynthetic machinery extends to chloroplast components, including electron transport and carbon fixation processes (Jahan et al., 2021; Habibi, 2021). This interaction enhances photosynthetic efficiency, ameliorating the adverse effects of salinity-induced perturbations on the photosystems and associated enzymatic activities. The regulatory effects of NO on both stomatal regulation and photosynthesis collectively facilitate a dynamic balance between water conservation and energy acquisition, culminating in enhanced adaptive strategies for plants confronting salinity stress. NO also exerts a multifaceted influence on key photosynthetic components, orchestrating their activities to mitigate the adverse impact of high salt concentrations. By interacting with enzymes like ribulose-1, 5-bisphosphate carboxylase/oxygenase (RuBisCO), NO enhances the efficiency of carbon fixation and assimilation, counteracting the potential impairment of CO₂ fixation caused by salinity (Fatma et al., 2016; Sehar et al., 2019). Furthermore, NO interacts with electron transport chain components, including cytochrome *b6f* and ferredoxin-NADP + reductase (FNR), bolstering electron flow and mitigating the disruption of electron transport caused by ionic imbalances (Mishina et al., 2007; Wei et al., 2014; Iyanagi, 2022). NO's regulatory impact extends to enzymes involved in the Calvin cycle, ensuring the sustained operation of crucial photosynthetic reactions under salinity-induced constraints (Wu et al., 2019). NO protects photosynthetic pigments and, thus, enhances the photosynthetic capacity in leaves. In tomato seedlings, NO application improved the Fv/Fm, qP, and actual ϕ PS II and reduced the NPQ coefficient, indicating the potential of NO to alleviate salt stress by

protecting photosystems (Wei et al., 2022). In this intricate interplay, NO emerges as a critical modulator, finely tuning photosynthetic enzyme activities to maintain energy production, carbon assimilation, and overall plant productivity in the face of salinity stress.

Moreover, NO may stimulate the activity of plasma membrane-associated PLD (Phospholipase D), responsible for the generation of polyamine (PA) by hydrolysing membrane lipids. PA stimulates the activity of tonoplast H⁺-ATPase via other signalling cascades (Guo et al., 2005). Pre-treatment of NO under salt stress enhances the total soluble protein content and endopeptidase and carboxypeptidase activities in plants, maintaining a balance between carbon and nitrogen metabolism (Zheng et al., 2010). Salt stress increased the soluble sugar content, further enhanced by the exogenous application of NO in the leaves of wheat plants. The accelerated accumulation of soluble sugar facilitates the cells to ameliorate salt stress by increasing osmotic pressure (Tian et al., 2015).

4. Crosstalk of NO with phytohormones

Plants encounter various perturbations in natural ecosystems, and concurrent exposure to stressors of diverse nature results in morphophysiological adaptation, thereby exacerbating the competence to endure. Therefore, plants have evolved with various adaptations to counteract the multifactorial disturbances, and a variety of signals function in a coordinated manner, allowing the plants to survive even under extreme stresses (Shahzad et al., 2021). Plants constantly fine-tune their cellular status with the exterior environment for optimised development by a complex, interconnected, and organised network of regulatory proteins and signalling molecules (Huang et al., 2022; Jang et al., 2020; Durbak et al., 2012). Phytohormones constitute an imperative class of signalling molecules which operate through diverse channels conferring plasticity to constantly transforming developmental as well as environmental cues in addition to helping the plants to adapt to the same (Aftab and Roychoudhury, 2021; Ali et al., 2020; Per et al., 2018).

NO is a ubiquitous endogenous signalling molecule during many pathophysiological phenomena in plants. Even though its substantial influence on the immunity of plants is quite established, precise information regarding the elaborative signal transduction cascades and crosstalk with other phyto-regulators and other intervening regulatory molecules involved in the defence responses to diverse stresses is still quite limited.

4.1. Nitric oxide and auxins

Insights into the auxin-NO interplay are imperative during the plant's diverse developmental and stress-related phenomena. Sufficient evidence regarding the exogenous sourcing of auxins (IAA) and concurrent increase in the endogenous level of NO in the hypocotyl region of *Cucumis sativus* is present where new meristems eventually arise and give birth to new explants (Pagnussat et al., 2004). Likewise, auxin (IBA) supplementation has enhanced NO accumulation in *Oryza sativa* roots (Chen and Kao, 2012). Auxin and NO operate cooperatively during different abiotic stresses, notably salinity and heavy metal stresses. Reports reveal that NO supplementation discourages the auxin-degrading enzymes, particularly IAA oxidase, thereby lessening the effects of stress on growth. The same has been observed in various plants exposed to stresses of different types like *Medicago truncatula*, *Triticum aestivum* and *Secale cereale* (Xu et al., 2010; Bethke et al., 2004b). The auxin-NO interplay becomes operational during the enhancement in the ferric-chelate reductase activity in *Arabidopsis* facing Fe deficiency (Chen et al., 2010). Furthermore, NO-induced auxin biosynthesis stimulates adventitious and lateral root formation in *Arabidopsis thaliana* exposed to salinity stress (Fahad et al., 2015; Chen and Kao, 2012). However, metal stressors-induced NO accumulation suppresses the accumulation of auxins and auxin carriers (PIN1/3/7), leading to an

alteration in the auxin homeostasis. An analogous mechanism is operative during salinity stress where salinity-induced NO accumulation modulates auxin-mediated developmental changes, notably reduced root-meristem size (Yuan and Huang, 2016; Liu et al., 2015). Furthermore, the auxin-NO crosstalk involves the interplay with ABA during the salinity stress as the NO-signalling upregulates certain antioxidant and ABA and Mo-dependent enzymes, which are decisive factors for mitigating the deleterious salinity effects (Santos et al., 2020). Molecular studies have been carried out to decode the auxin-NO interplay and the role of different proteins in auxin perception and signal transmission after that. AUXIN SIGNALLING F-BOX (AFBs) and TRANSPORT INHIBITOR RESPONSE 1 (TIR1) proteins bind auxins and degrade specific transcriptional repressor proteins (AUX/IAA) with the help of 26 S proteasome, facilitating several plant developmental phenomena. NO is critical during this signalling event as it carries out S-nitrosylation of TIR1 at a particular cysteine residue (Cys-140), bringing out more effective degradation of the repressor, AUX/IAA (Terrile et al., 2012).

4.2. Nitric oxide interplay with cytokinins

Research during the last decade has accrued significant evidence regarding the multifaceted interactions between cytokinins (CKs) and NO, signifying both antagonistic and synergistic interplay between them depending on the plant species under study and the conditions responsible for the physiological response in the plant. Studies confirm both increased, decreased, and unchanged NO levels upon exogenous CK application (Freschi, 2013). The synergistic interplay of the two phytohormones has been validated in diverse plant responses like drought adaptability, cell division, regulation of senescence and photosynthesis and cell differentiation (Shen et al., 2013; Shao et al., 2010). Precocious senescence in detached as well as intact leaves in transgenic or NO-deficient mutants has been reported (Mishina et al., 2007). Moreover, photosynthetic down-regulation in NO-degrading dioxygenase-expressing Arabidopsis exemplified by senescence-like phenotype is reportedly overcome by CK application (Mishina et al., 2007). The synergistic interplay during the cell cycle regulation can be manifested from NO deficient callus displaying severe down-regulation of CYCLIN-D 3; 1, a cell cycle progression-inducing gene attenuated by CKs at the transcriptional level (Shen et al., 2013). Reports reveal that salinity results in enhanced endogenous CKs levels, and exogenous application of CKs alleviates salinity-induced damage in many plants (Feng et al., 2019; Keshishian et al., 2018; Joshi et al., 2018; Prerostova et al., 2017). Like drought stress, CKs might involve synergistic interplay with the NO during salinity stress alleviation owing to the positive role of NO in salt stress mitigation; however, no report of such interplay is available to date.

Like auxins, CKs and NO interact antagonistically in the guard cells of *Vicia faba*, resulting in stomatal opening during the dark hours. Applying CKs eliminates SNP-induced NO production, reducing the endogenous NO levels in the guard cells, thereby reversing the stomatal closure in the darkness (Xiao-Ping and Xi-Gui, 2006). The antagonistic interaction has also been validated in transgenic tobacco (Wilhelmova et al., 2006). Furthermore, reports signify that NO concentrations in plants negatively impact endogenous CK levels because of the affinity of the strong affinity of peroxynitrite (a NO derivative) with zeatin, rendering the CKs unavailable (Liu et al., 2013).

4.3. Nitric oxide interplay with gibberellins

Gibberellic acid is vital in mitigating salinity-induced deleterious effects in plants through the modulation of photosynthesis, antioxidative metabolism, osmolyte accumulation, and ionic homeostasis (Shahzad et al., 2021; Tsegay and Andargie, 2018). GA and NO interplay has been validated during some plant physiological phenomena and abiotic stress, particularly salinity stress (Chen et al., 2022; Sanz et al., 2015; Lozano-Juste and León, 2011; Achard et al., 2006). The two

signalling components interact antagonistically, as is evident from the NO-mediated accumulation of repressors of GA signalling, specifically DELLA proteins, consequently repressing the GA signalling pathway. Furthermore, the antagonism finds validation from NO-induced down-regulation of GA2Oxidase3, a vital GA biosynthesis enzyme encoding gene (Lozano-Juste and León, 2011). During salinity stress, GA-induced growth promotion involves transcriptional repressor-degradation, noteworthy among which is the proteasomal-degradation of DELLA repressors (Chen et al., 2022).

Furthermore, salinity stress induces NO accumulation, leading to increased salt tolerance. Such a salinity tolerance relies upon an imperative post-translational modification mediated by NO, which involves S-nitrosylation of Cys-374 of RGA protein, a key DELLA member. Consequently, this nitrosylation restrains the RGA protein interaction with another vital signalling component, SLY1, an F-box protein, thus preventing proteasomal degradation during salinity stress. Such an accumulation of RGA subsequently retards growth but increases tolerance against salinity (Chen et al., 2022). Therefore, GA signalling is negatively regulated via NO-induced S-nitrosylation of RGA to coordinate the equilibrium between growth and stress (Chen et al., 2022). Synergistic interplay has, however, been reported between GA and NO during Al stressed-wheat plants where SNP stimulated GA accumulation and apical root growth (He et al., 2012).

4.4. Nitric oxide and ethylene

Nitric oxide (NO) and ethylene (ET) are noteworthy gaseous phytohormones and multifunctional signals involved in diverse metabolic and developmental phenomena in plants (Freschi, 2013; Manjunatha et al., 2012). A considerable number of presently available studies on the NO and ETH interplay reveal a negative association in regulating multiple growth and developmental aspects, noteworthy among which are fruit ripening and regulation of senescence (leaf and flower) (Manjunatha et al., 2012; Lamattina et al., 2003; Leshem and Pinchasov, 2000). The antagonistic biosynthetic trend has been validated through studies involving measurements of ETH and NO emissions during plant senescence as well as fruit ripening (Freschi, 2013; Corpas et al., 2004; Leshem and Pinchasov, 2000). Exogenous sourcing and depletion of ETH in Olive fruits led to the suppression and promotion of NO, respectively, signifying the negative impact of ETH on the endogenous NO concentration (Freschi, 2013; Parra-Lobato and Gomez-Jimenez, 2011). Furthermore, reports have confirmed that NO-induced inhibition in ethylene production in fruit ripening is endorsed to down-regulation of vital ETH biosynthetic enzymes and/or diminution in their transcript level (Manjunatha et al., 2012).

Evidence of NO stimulating ETH production is also well established, as has been reported in the non-senescent leaf tissues of plants like *Arabidopsis*, tobacco, and maize (Ederli et al., 2006; Mur et al., 2009). NO donors stimulate gene expression of ETH biosynthetic enzymes like ACS, SAM, ACOs, and MTK (Garcia et al., 2011; Mur et al., 2009; Ederli et al., 2006). A biosynthetic link between the two is manifested from the existence of the same precursor for ETH and polyamines and the production of NO from the oxidation of polyamines, connoting a metabolic link between ETH and NO. ETH regulating the expression of H⁺-ATPase during abiotic stress and NO inducing the biosynthesis of ETH during the breakage of dormancy as well as under ozone stress is well established (Freschi, 2013; Gniazdowska et al., 2007; Waters et al., 2007; Lucena et al., 2006; Ederli et al., 2006). ETH and NO act synergistically to fiddle with the ion homeostasis by attenuating the plasma membrane H⁺-ATPase during salinity stress, where ETH acts as an imperative downstream component of the NO signalling pathway (Wang et al., 2009). Furthermore, ETH/NO interplay allows proficient nitrogen and sulphur utilisation, benefitting carbon assimilation and yield potential in plants encountering salt stress, thereby enhancing endurance by increased synthesis of required metabolites (Jahan et al., 2021).

4.5. Nitric oxide and abscisic acid

Abscisic acid (ABA) is critical to induce numerous plant adaptations against perturbations of diverse nature including salinity, temperature, drought, and osmotic stresses (Xu et al., 2022; Li et al., 2020). Plants exposed to salinity exhibit a rapid increase in the endogenous ABA concentration that can regulate the assimilates translocation, the guard cells ion fluxes for stomatal closure, and gene expression (Wei et al., 2020; Wu et al., 2019; Wang et al., 2020; Parida and Das, 2005; Jia et al., 2002). Like many other stresses, salinity upregulates the expression of an essential ABA biosynthetic gene 9-cis-epoxycarotenoid dioxygenase, increasing endogenous ABA concentrations; however, the ABA accumulation depends upon the severity of stress (Mulholland et al., 2003).

The ABA and NO interplay reveal the hand-and-glove relationship between NO and ABA, particularly during stress-induced stomatal closure (León et al., 2014; Bright et al., 2006). NO substantially impacts the ABA-induced accumulation of osmolytes and fortification of the antioxidant system in plants facing oxidative stress, as revealed by the study using NO inhibitor cPTIO (2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazole-1-oxyl-3-oxide) in wheat (Iqbal et al., 2022). Moreover, NO production in plants is vital for ABA-induced stomatal closure, and exogenous ABA application stimulates NO biosynthesis within the guard cells (León et al., 2014; Neill et al., 2002). Release of Ca^{2+} from the *Vicia faba* guard cells governs the regulation of the activity of K^+ channels ending up in stomata closure (García-Mata et al., 2003). ABA and NO display a synergistic approach stimulating the synthesis of each other. Salinity diminishes sucrose accumulation, photosynthetic reserves, and an antioxidant system accredited to downregulate the activities of NADP-malic enzyme, ascorbate peroxidase, and glutathione S-transferase in rice. NO (applied as SNP, an NO donor) and ABA application effectively alleviated the NaCl-induced deleterious effects, and the finding is elucidative of NO and ABA acting either cumulatively or independently (Saha et al., 2022; León et al., 2014). Studies using NO inhibitors have ascertained that NO stimulates ABA biosynthesis in different plants, as is evident from the cPTIO-induced blockade of stomatal closure induced by ABA. Likewise, ABA enhances endogenous NO content in wheat, broad bean, and pea (Iqbal et al., 2022; Neill et al., 2002). NO-induced ABA synthesis involves NO-mediated activation of a phosphatase enzyme protein phosphatase 2C (PPC), which promotes the binding and stability of an ABA-receptor complex. Studies involving PPC mutants have elucidated the failure of NO-induced stomatal closure in plants, signifying that PPC should be an essential but downstream component of the NO signalling pathway (Santos et al., 2020; Desikan et al., 2002).

Furthermore, NO interacts with the ABA transcription factors (ABI1, ABI5) through S-nitrosylation, promoting their activity (Albertos et al., 2015; León et al., 2014; Dubovskaya et al., 2011). NO may also induce the inactivation of ABA receptors via nitration of specific tyrosine residues, which have been proposed to be crucial cellular adjustments in response to ABA, particularly during the simultaneous production of NO and ROS in the cell (Castillo et al., 2015). NO ABA interplay becomes operational even during the regulation of CAM metabolism, ensuring the survival of plants facing nutrient and water-limited conditions (Mito and Mercier, 2013; Freschi et al., 2010). Moreover, the interplay becomes intensive in plants facing environmental perturbations, stimulating diverse adaptive responses like an antioxidant defence system and stomatal closure (León et al., 2014; Tossi et al., 2009; Neill et al., 2008).

4.6. Nitric oxide and jasmonates

Jasmonates (JAs) constitute an imperative class of phytohormones known for their regulatory role in plants exposed to environmental cues of varied types, including salinity (Jang et al., 2020; Yang and Guo, 2018; Wasternack et al., 2006). Scanty literature exists about the interaction of NO and JAs in abiotic stress tolerance; only a few JA-stimulated signalling reactions find an association with NO signalling

components. Plants exposed to salinity exhibit increased JAs accretion by inducing the expression of genes related to JA biosynthesis (Yang and Guo, 2018; Du et al., 2013; Tanou et al., 2009). NO plays a critical regulatory role in JA biosynthesis by upregulating the expression of imperative JA biosynthetic enzymes in *Arabidopsis thaliana*, like lipoxygenase and allene oxide synthase (Huang et al., 2004). In yet another study, upregulated expression of JA biosynthetic genes, notably LOX3 (At1g17420), OPR 1, 2, 3, has been reported (Palavan-Unsal and Arisan, 2009; Mur et al., 2009; 2013). However, the negative role of NO on the expression of AOC, another JA biosynthesis gene, has been reported (Kazan and Manners, 2012; Palavan-Unsal and Arisan, 2009). The inhibitory effect of NO on AOC is due to S-nitrosylation (Romero-Puertas et al., 2008). Furthermore, a study using a NO-synthase inhibitor (NG-nitro-L-arginine methyl ester) revealed JA-induced stomatal closure, signifying the operation of NO downstream of JA (Liu et al., 2005). Moreover, JAs sourced exogenously results in decreased Na^+ ion content in plants (Qiu et al., 2020; Du et al., 2013; Tanou et al., 2009) and attenuated salt-induced deleterious effects (Javid et al., 2011; Yoon et al., 2009). Evidence concerning the synergistic interaction of NO and JAs in plants does exist (Jang et al., 2020; Yang and Guo, 2018; Hsu et al., 2013). JAs application to *Oryza sativa* roots stimulates NO production, as has been confirmed using NO scavenger cPTIO (Hsu et al., 2013). However, further research is needed to elucidate the interplay of NO and JAs in salinity-induced tolerance.

4.7. Nitric oxide and salicylic acid

SA and NO are well-established phyto regulators which attenuate salinity tolerance in many crops like pea, wheat, red mung bean, and tomato (Ahanger et al., 2019; Yadu et al., 2017; Naser Alavi et al., 2014; Gémes et al., 2011). While salinity is known to inhibit seed germination, Jini and Joseph (2017) found SA treatment encourages seed germination in Indica rice varieties. Exogenous SA application improved endogenous SA levels in such plants and palliated Na^+ and Cl^- accumulation. SA helps with osmotic regulation (Miura and Tada, 2014), ROS regulation (Torun et al., 2024), ion homeostasis (Nie et al., 2018) and stomatal regulation (Zamora et al., 2021) in plants affected by salinity stress. Salinity tolerance can result from the interplay between SA, NO, and NaCl-generated ROS, as Gémes et al. (2011) reported in tomato. A decrease in the H_2O_2 and NO concentration in salinity-affected tomato is an outcome of generating free radicals. Exogenous sourcing of SA attenuates the salt stress response by lowering the free radicals leading to a rise in the endogenous accumulation of NO (Kaya et al., 2020; Gémes et al., 2011; Molassiotis et al., 2016). A study used NO scavenger cPTIO to abolish the SA-induced NO production, confirming whether SA application in pepper plants triggers endogenous NO production during salt stress. The cPTIO application and SA rendered the alleviatory effect of SA ineffective, clarifying the role of SA in attenuating salinity tolerance involves NO acting as a downstream signal in the SA-induced signalling pathway. Such a NO-induced salt endurance has been reported in other plants like chickpea and mung bean (Kaya et al., 2020; Ahmad et al., 2016). NO plays an imperative role in SA-mediated salinity endurance in plants by modulating different antioxidants, particularly the ascorbate-glutathione cycle (Kaya et al., 2020). Evidence in support comes from the study of Kaya et al. (2020), who has observed the reversal of the SA-induced high ratios of GSH/GSSG and AsA/DHA in the presence of NO scavenger. Further evidence comes from the study of Ahanger et al. (2019) in *Vigna angularis*, where joint-application NO and SA alleviated salinity stress by regulating photosynthesis and antioxidant system predominantly ASH-GSH cycle.

NO and SA crosstalk may have a positive or negative correlation depending on metabolic circumstances. Reports reveal that exogenously provided NO is closely associated with the biosynthesis of SA, and SA, in turn, is linked with H_2O_2 and NO biosynthesis (Rivas-San Vicente and Plasencia, 2011; Song and Goodman, 2001; Campos et al., 2019). SA has an up-regulatory effect on the nitric oxide synthase activity, as

confirmed through the mutant studies in *Arabidopsis*, thereby enhancing NO production (Zottini et al., 2007). NO and ROS display a close relationship during SA-induced changes in response to oxidative stress in *Arabidopsis*. SA-induced NO and ROS production in the stomatal guard cells is an outcome of the increased peroxidase activity and disabled K^+ channels inducing the stomatal closure (Khokon et al., 2011). SA-induced alterations in redox homeostasis lead to a swift conformational change in NPR1 (*non-expressor of pathogenesis-related gene 1*) by splitting the intermolecular disulphide linkages, which converts it from an inactive oligomeric form to an active monomeric form. Once activated, the monomeric form is bound by the TGA1 transcription factor and is directed to the nucleus to upregulate certain stress-related genes (Asgher et al., 2017; Palavan-Unsal and Arisan, 2009). The oligomeric and monomeric forms result from S-nitrosylation of specific cysteine residues; whereas Cys-156 of NPR1 is nitrosylated during oligomerisation, Cys-172 and Cys-287 are nitrosylated during redox-induced monomerisation (Asgher et al., 2017; Palavan-Unsal and Arisan, 2009). The effective conformational change in TGA1, which allows its binding to the NPR1, is accredited S-nitroso glutathione. NO-SA crosstalk can also be observed during NO-induced oxidative damage wherein SA induces the upregulation of salicylic acid-binding protein 3, an enzyme that is associated with the hydration of CO_2 -generating protons and bicarbonate ions, which can bind to SA further and re-establish the redox homeostasis (Ahanger et al., 2019; Palavan-Unsal and Arisan, 2009). SA and NO act as vital signalling compounds necessary to trigger the plant's innate immunity against stressors of diverse types, partly by transcriptional reprogramming of various secondary metabolite-producing, defence-related and anti-microbial genes and partly by fortifying anti-oxidative metabolism (Ahanger et al., 2019; Ageeva-Kieferle et al., 2019; Agarwal et al., 2016). Such a transcriptional regulation is imperative to fine-tune various other vital metabolic functions to create an impenetrable and resilient immune response during the circumstances of active plant growth suppression due to perturbed external and internal environments (Ahanger et al., 2019; Ageeva-Kieferle et al., 2019; Agarwal et al., 2016).

4.8. Nitric oxide and melatonin

Melatonin, chemically N-acetyl-5-methoxytryptamine, is a ubiquitous phyto-regulator having a structural resemblance with indole-3-acetic acid and regulates various aspects of plant growth and development (Nawaz et al., 2016). Melatonin acts as a master regulator during abiotic stress tolerance reactions by modulating the expression of various downstream genes (Wang et al., 2009). As a stress-regulator, melatonin functions as an antioxidant to scavenge diverse reactive species and free radicals (H_2O_2 , HO^{\cdot} , NO, ONOO $^{\cdot}$, HOCl, 1O_2), thereby serving the protective function during extreme environments (Tanou et al., 2009). The biological character of melatonin has, however, changed during its evolution from an antioxidant to a hormone (Arnao and Hernández-Ruiz, 2018; Zhu et al., 2019). Melatonin-mediated stress response includes melatonin-induced stimulation of specific G-protein coupled receptor (CAND2), activating H_2O_2 and Ca^{2+} signal transduction, leading to stomatal closure (Wei et al., 2014).

What has fascinated physiologists is the addition of nitrogen atoms to the indole moiety of melatonin, resulting in the formation of N-nitroso melatonin, which functions as a binding signalling molecule during the maintenance of redox homeostasis (Mukherjee, 2019; Singh et al., 2016). Exogenously sourced melatonin has been observed to increase the endogenous NO concentration by up-regulation and down-regulation of nitrate reductase and S-nitroso glutathione reductase enzymes, respectively (Esmaeili et al., 2023). Moreover, accumulative melatonin serves an antioxidant role during the ripening of tomato and scavenges free nitrogen species (Corpas et al., 2018). cGMP upregulates the NO-mediated biosynthesis of melatonin as revealed by enhancement in cGMP levels by SNP-induced repression of aryl-alkylamine-N-acetyltransferase activity (Wellard and Morgan,

2004). Furthermore, melatonin and 2-hydroxy melatonin, an anti-stress derivative of melatonin, have been endorsed for chilling and drought tolerance in tomato and tobacco by eliciting arginine-dependent NO accumulation (Aghdam et al., 2019; Lee and Back, 2016).

Exogenous melatonin application in various types of plant seedlings overcomes the ill effects of salinity stress by subsequent enhancement in the endogenous melatonin concentration, which in turn is endorsed to increase in the photosynthetic attributes, notably total chlorophyll content, net photosynthetic rate and maximum PSII quantum efficiency (Zhang et al., 2014). Melatonin increases the salinity endurance by partaking via the ROS signalling route, as revealed from the melatonin-triggered reestablishment of ion and redox homeostasis in a respiratory burst oxidase protein F *Arabidopsis* mutant (Chen et al., 2017). The location of ROS upstream of NO strengthens the fact that NO/melatonin balances ROS production and regulates the signals of oxidative resistance in plants. NO-releasing compounds like SNP and melatonin regulate the gene expression of the NHX1 (sodium hydrogen exchanger) as well as SOS2 (salt overly sensitive 2) at the transcription level, thus optimising the Na^+/K^+ ratio (Zhao et al., 2018). Glutathione, an antioxidant and electron-donor with high intracellular concentration, indicates the cellular oxidative status and the ratio of its reduced to oxidised form (GSH/GSSG) is maintained by an essential enzyme glutathione reductase (Foyer et al., 2001). Alleviation of salinity-induced toxicity in sunflower due to melatonin and NO has been accredited to increased GSH content and GR activity (Kaur and Bhatla, 2016).

SNP has been observed to repress the activity of a melatonin synthase enzyme, hydroxyindole-O-methyltransferase; however, the same was upregulated in salt-stressed sunflower seedlings. The cooperative action of melatonin and NO in salinity stress mitigation has been reported in pepper, where leaf-applied melatonin increased the endogenous NO and H_2S levels, and NO and H_2S act downstream of the melatonin during the signal transduction pathway (Kaya et al., 2019). NO-melatonin interaction operates as a long-distance signal and maintains oxidative homeostasis in collaboration with two SOD isoforms (Mn-SOD and Cu/Zn-SOD) (Arora and Bhatla, 2017). Furthermore, the decreased Na^+ accumulation and fortified antioxidant system due to melatonin are endorsed to increase NO concentration and eventually increase the salinity tolerance (Liu et al., 2015).

Melatonin enhances plant immunity by stimulating mitogen-activated protein kinase 3 and oxidative signal-inducible1 by signalling crosstalk with NO (Lee and Back, 2016, 2017). Melatonin signalling leads to the activation of mitogen-activated protein kinase (MAPK) and cyclic adenosine monophosphate (cAMP) signal transduction pathways via NO (Ding et al., 2018). In addition to NO, melatonin treatment has also been reported to increase endogenous SA concentration, which is acknowledged for its role in plant stress mitigation (Zhao et al., 2018, 2019). Some other imperative aspects of melatonin-NO interaction include H_2O_2 as a vital mediator and post-translational protein modification through S-nitrosylation, phosphorylation or glycosylation (Arnao and Hernández-Ruiz, 2019).

5. Crosstalk of NO with reactive oxygen and reactive sulphur species

Production of ROS and reactive sulphur species (RSS) is an inevitable phenomenon during stressful conditions, and this interplay with NO is well established (Corpas, 2019; Kaur et al., 2019; Corpas et al., 2020; Sandalio et al., 2023). The most common and widespread ROS in plants include hydroxyl radical ($^{\cdot}OH$), hydrogen peroxide (H_2O_2) and superoxide anion ($O_2^{\cdot-}$) (Kalia et al., 2017; Corpas et al., 2020). NO signal-crosstalk with ROS involves binding with the heme-prosthetic group of ROS-scavenging enzymes (e.g., CAT, Fe-SOD). Moreover, being highly reactive and lipophilic, NO modulates enzyme activities with metallic co-factors (Arora et al., 2016). H_2O_2 and NO interplay is further validated by Liu et al. (2020) in tomato, wherein

trehalose-induced lipid-peroxidation was significantly diminished after the application of NO and H₂O₂ scavengers, cPTIO and dimethyl thiourea (DMTU), respectively, signifying the possibility of trehalose-induced NO and H₂O₂ biosynthesis, particularly during stressful conditions. In addition, SNP pre-treated roots of *Citrus aurantium* L. display increased H₂O₂ and NO-induced salinity acclimation (Molassiotis et al., 2016). H₂O₂ overproduction promotes osmolyte accumulation through NO downstream signalling (Wang et al., 2020c).

The role of NO in mitigating salinity-induced toxicity, as confirmed by the studies using NO-donors and inhibitors, has been correlated with the ratio of cytosolic Na⁺/K⁺ ratio. The cytosolic Na⁺/K⁺ ratio is regulated by the plasma membrane (H⁺-ATPase) and vacuolar (H⁺-PPase) protein activities along with defence-related and antioxidant genes (Zhao et al., 2004; Y.Q. Wang et al., 2009; Zhang et al., 2009; Uchida et al., 2002). Further, NO can positively influence ROS and antioxidant metabolism (Arora et al., 2016; Shi and Chan, 2014). Besides, salinity-exposed plants have been witnessed to display H₂O₂-induced up-regulation of stress-related genes (Miller et al., 2010). The ROS and NO-triggered changes are not limited to the tissues produced, as confirmed by the study in which H₂O₂ and NO supplementation to roots trimmed down the NaCl-induced physiological disproportion in citrus leaves (Tanou et al., 2009).

Salinity alters the activities of plant guard-cell signalling compounds, notably Ca²⁺, ABA, NO, and ROS, regulating the stomatal opening and closing (Hasanuzzaman et al., 2018). Studies carried out on mangrove plants revealed interplay between imperative oxidative stress-signalling intermediates, Ca²⁺, NO and ROS, elucidating that the increased extrusion of deleterious Na⁺ is endorsed to NO-induced stimulation of Na⁺/H⁺ antiporters (Lang et al., 2014). Furthermore, NO-induced stimulation of Ca²⁺ signalling has been validated in *Vicia faba* guard cells; NO controls guard cell movement by governing cytosolic Ca²⁺ content via Ca²⁺ channels (Garcia-Mata et al., 2003).

The interplay between H₂S (RSS) and NO is a significant aspect of diverse developmental phenomena under normal and perturbed environmental conditions (Kaya et al., 2020; Chen et al., 2015, 2016). The signalling crosstalk becomes operational during abiotic stress tolerance, such as wheat tolerance against Cd (reviewed by Mukherjee and Corpas, 2020). H₂S and NO interaction stimulate the essential mineral uptake, the antioxidative defence system, to reduce the root uptake of Cd and associated oxidative damage in wheat (Kaya et al., 2020). Another important outcome of H₂S and NO signalling is the generation of an intermediate sulphur analogue, persulfide, known to regulate the contents of ROS and RNS in plants (Lisjak et al., 2013). Increased NO accumulation and associated adventitious root formation in NaHS-treated sweet potato suggests NO is a downstream signalling component of H₂S (Zhang et al., 2009).

6. Conclusions and future trends

NO regulates a wide range of phenomena corresponding to normal growth and development. These phenomena are underpinned by the intricate correspondence of NO with phytohormones. Such as NO regulates stomatal dynamics mainly through ABA and, to some extent, IAA and CKs. Similarly, several defence responses are elicited by NO-spiked JA and SA. Furthermore, GAs, ET, and melatonin mediate NO influence over cellular growth, maturity and ripening, and enzymatic antioxidant functionality. It is evident that phytohormones are one of the leading chariots of NO-induced upgradation of plant biochemistry and stress physiology during salinity. Apart from the NO-phytohormones interface, it is high time to explore the NO relation with ROS and RSS. While ROS have established potential in domineering salinity-induced oxidative stress, studies on RSS-NO interface are scarce. Future trends can explore how NO operates with RSS and what signals facilitate the correspondence. Furthermore, growing empirical studies have suggested NO's extensive role in the signal transduction of various metabolic pathways corresponding to normal plant physiology.

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Declaration of competing interest

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